Motility and calcareous parts in extant and fossil Acrothoracica (Crustacea: Cirripedia), based primarily upon new species burrowing in the deep-sea scleractinian coral *Enallopsammia*

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Abstract.   Four new species of bathyal acrothoracican barnacles of the family Lithoglyptidae are described: *Lithoglyptes viatrix* from Hawaii, *L. tectoscrobis* and *Weltneria ligamenta* from Tonga, and *W. griggi* from the Caribbean island of Grenada. All burrow in ahermatypic corals of the genus *Enallopsammia*. Because rostra are very rare in the Acrothoracica, the rostra and calcareous cement possessed by at least three of these species are of particular interest. Instead of serving simply to attach the barnacle to the burrow wall, they may be modified into a roof (or trail) sealing the apertural slit left behind as the barnacle bores across the coral surface. This system is so highly developed in *L. viatrix* that some specimens are truly motile and abandon the older parts of their burrows. Other rostral structures in living and fossil acrothoracicans are reviewed, and criteria are given to distinguish rostra from calcareous cement. Analogous systems of calcareous structures (cement only) and apertural motility in the families Cryptophialidae and Trypetesidae, and in various fossil genera are also discussed; apparently none of these acrothoracicans abandon any part of their burrows, although the bulk of the mantle may move a considerable distance. A general trend towards loss of the rostrum and calcareous cement is evident in extant and fossil Acrothoracica that live in shallow environments, but at different stages of reduction the remaining calcareous parts often have been independently modified to protect the mantle as the aperture moves to a more favorable position in the substrate. Calcareous parts in fossil acrothoracican burrows are not always ichnofossils, but may be true body fossils, a fact which has nomenclatural significance.

INTRODUCTION

The Acrothoracica are burrowing barnacles and most species live in shallow water in calcareous substrates such as coral skeletons and mollusk shells (Tomlinson 1969). Their fossil record, almost exclusively in the form of burrows or casts of burrows, extends back into the Devonian (Rodriguez and Gutschick 1977). The exterior of an adult acrothoracican consists of a sac-like mantle or carapace, and an attachment disc. The mantle usually lacks hard parts except for a pair of chitinous opercular bars guarding the mantle opening (Newman 1971). The acrothoracicans are further distinguished from ordinary barnacles in having all but the first pair of cirri (mouth cirri or maxillipeds) clustered at the rear end of the thorax. Two suborders and three families are generally recognized: Pygophora (Lithoglyptidae, Cryptophialidae) with an anus and biramous terminal cirri, and Apygophora (Trypetesidae) without an anus and with unbranched cirri.

This paper concerns four new species of relatively large lithoglyptid acrothoracicans that burrow in living and recently dead branches of the bathyal ahermatypic coral *Enallopsammia*. These new species have an unusually deep habitat, and at least 3 of them possess a rostral plate, a very rare feature in this order (Newman 1971, 1974). Furthermore, at least one of these species, *Lithoglyptes viatrix,* is capable of a unique sort of limited motility. Our efforts to understand the rostrum and its role in motility

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in *L. viatrix* led us to investigate other types of calcareous structures and modes of motility in living and fossil Acrothoracica.

METHODS AND MATERIALS

Coral specimens housing the acrothoracicans were obtained from R. W. Grigg (Hawaii Institute of Marine Biology), and the National Museum of Natural History (USNM) in order to study galls formed on them by ascothoracid crustacean parasites of the family Petrarcidae (Grygier 1981, Zibrowius and Grygier, in prep.). Collection data accompany each species description given below. Acrothoracicans were detected by the characteristic apertures of the burrows and, in some cases, by the presence of light-colored streaks extending across the surface of the coral branches (Fig. 2).

Most of the barnacles had been dried. Those to be dissected were reconditioned in a weak trisodium phosphate solution for at least a day, either prior to or after extraction. Prior reconditioning gave better results. Animals were extracted from their burrows either by dissolution of the coral in dilute HNO_3 or by mechanically excising the surrounding coral with a hand-held, rotary tool (Moto-tool Model no. 1, Dremel Mfg. Co., Racine, Wisconsin) and diamond wheel. Later dissolutions were not carried to completion in order to save as much of the calcareous rostrum in situ as possible. Dissected parts and occasionally gut contents were examined in glycerine and glycerine jelly mounts. Drawings were done with cameras lucida on Wild M5 and M20 microscopes.

Occupied burrows of *Lithoglyptes viatrix* new species, *Australophialus melampygos* (Berndt), *L. spinatus* Tomlinson and Newman (cf. Newman and Tomlinson 1974), *Trypetesa lateralis* Tomlinson, and a new species of *Trypetesa* (Standing and Tomlinson, in prep.) were selected for special examination. Some burrows of each were excavated with the cutting wheel described above, or with needles and forceps. For *L. viatrix,* dimensions of apertures and exposed "trails" were measured with dividers and a slide micrometer. Frontal and sagittal thin sections of *L. viatrix* burrows were done according to Newman et al. (1969), except that blanks were cut on a low-speed saw (Isomet 11-1180, Buehler Ltd., Evanston, Illinois) equipped with a diamond cutting wheel.

TAXONOMY

Class Cirripedia Burmeister, 1834
Order Acrothoracica Gruvel, 1905
Family Lithoglyptidae Aurivillius, 1892

Tomlinson (1969) defined this family on the basis of the tapered burrow apertures, lack of a gizzard (gastric mill), possession of caudal appendages in some forms, well-developed mouth cirri, and a labrum proportionately comparable in size to the paired mouthparts, as in ordinary barnacles. All of these characters are plesiomorphies, as shown by comparison with other barnacles. Thus, this family is possibly paraphyletic. For the most part, lithoglyptid genera are defined by the presence or absence of caudal appendages and the number of terminal cirri (Table 1).

Variation in opercular bar armament is useful in distinguishing species, but there are essentially no other diagnostic characters available. The nonmonotypic genera of lithoglyptids must be suspected of paraphyly or polyphyly. But because of the unresolved polychotomies, we are continuing to employ the current, admittedly artificial classification for reasons of practicality.

Lithoglyptes Aurivillius, 1892

Diagnosis. —Lithoglyptids with four pairs of terminal cirri (III–VI) and a pair of caudal appendages (Table 1).
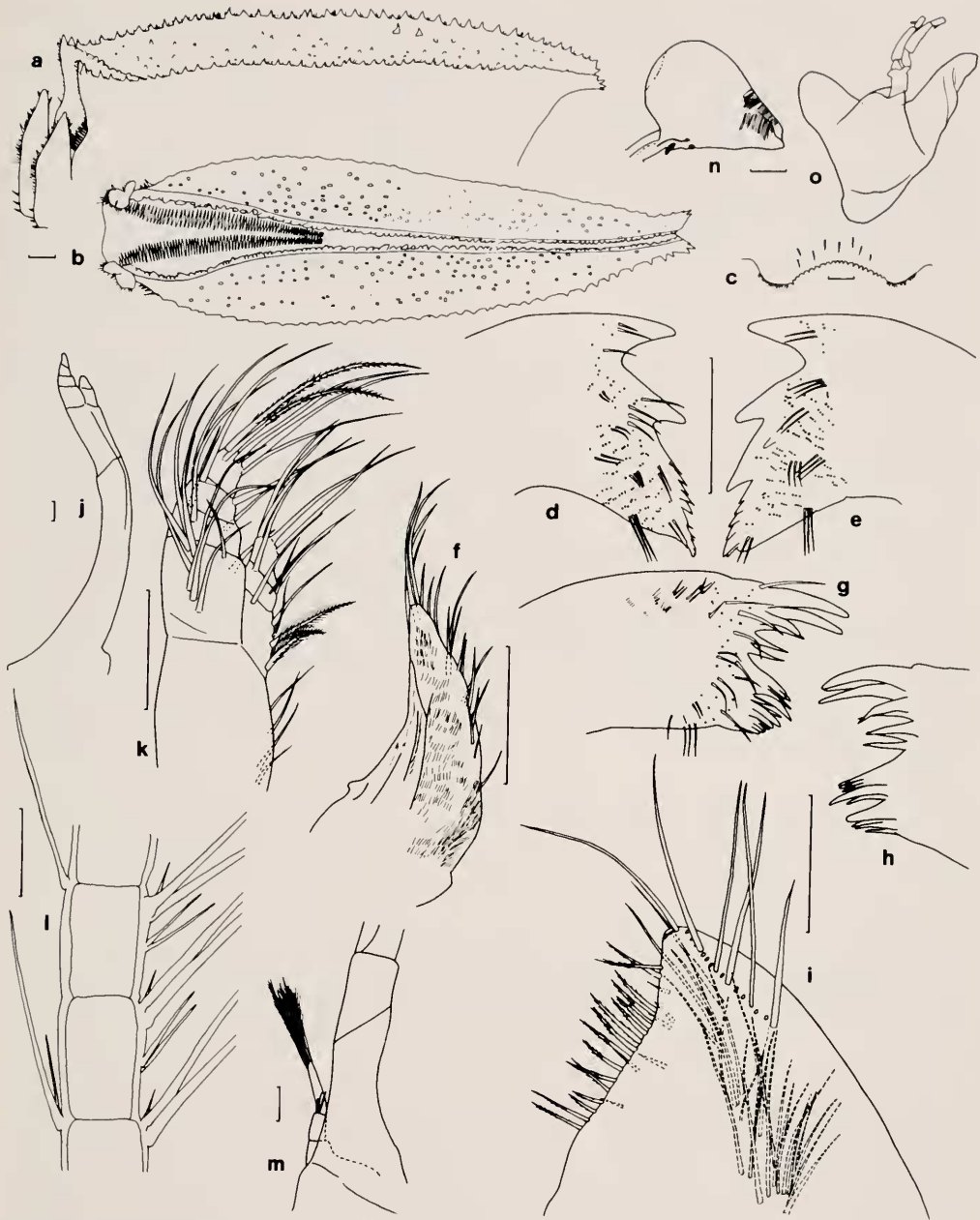
FIGURE 1. *Lithoglyptes viatrix* new species a–m, Females, dissected parts; a, b, Lateral and top view of opercular region of holotype, carinal end left; c, Labral crest, anterior view, flattened; d, e, Mandibular gnathobases, most setae omitted except for insertion sites; f, Mandibular palp; g, h, Maxillular gnathobases, setae omitted in h, most omitted in g but insertion sites shown; i, Maxilla, rear view; j, Mouth cirrus (I); k, Detail of different mouth cirrus (I), full setation not shown; l, Typical setation of central part of terminal cirrus (IV–VI); m, Protopod of left last cirrus (VI) and caudal appendage; n, o, Complemental males; n, Ventral view; o, Ventral view of different specimen. Scale bars 0.1 mm.

Lithoglyptes viatrix new species
Figures 1–4

Diagnosis. —Calcareous cement and a rostrum are present, although the form of the rostrum is variable and it may form a roof over an elongate, trench-like burrow.

TABLE 1. Distribution of thoracic appendages among lithoglyptid genera (MC, mouth cirrus or maxilliped; TC, terminal cirrus; CA, caudal appendage or furcal ramus).

	I	II	III	IV	V	VI	CA
Weltneria	MC	TC	TC	TC	TC	TC	CA
Berndtia	MC	TC	TC	TC	TC	TC	—
Lithoglyptes	MC	—	TC	TC	TC	TC	CA
Balanodytes	MC	—	TC	TC	TC	TC	—
Kochlorine and							
Kochlorinopsis	MC	—	—	TC	TC	TC	CA

The mantle is elongate, and the carinal margin is nearly straight rather than broadly curved. The first terminal cirrus (III) has the endopod longer than the exopod.

Material. —Approximately 21 whole and 3 partial females, and 2 males, in *Enallopsammia amphelioides* (Alcock) [Cairns (1982) considers this a synonym of *E. rostrata* (Pourtalès)] from 4 localities in the Hawaiian Islands (Table 2). All had been air-dried. Chamberlain's specimens from Oahu and Grigg's from Kaula Rock are chosen as type lots because they include most of the specimens examined. The dissected holotype from Kaula Rock (USNM 210849) and 5 paratypes from both localities (USNM 210850) are deposited in the National Museum of Natural History. Other paratypes are deposited in the British Museum (Natural History), Zoology and Palaeontology Departments (Reg. nos. 1984.140–144 and T814, respectively), the Bernice P. Bishop Museum, Honolulu (Cat. No. B510), the Institute for Paleontology, University of Vienna (IPUW-2523), the San Diego Natural History Museum, San Francisco State University, and the authors' collections.

Etymology. — From Latin *viator* (a traveler) with feminine suffix, referring to female motility.

Description. —Females: Operculum fusiform (Fig. 1a, b), that of holotype 2.1 mm long, 0.7 mm wide, wider toward carinal than rostral end, slightly smaller than burrow aperture. Sharp denticles interspersed with minute hairs along lateral edges of bars, faces with scattered papillae; closely-spaced, flat-topped papillae along medial edges. Comb collar between carinal halves of opercular bars.

Mantle long (5 specimens 4.3–7.5 mm), tapered, often bent nearly at right angle just below operculum (Fig. 4d–f); well-muscled, with small bifid or trifid spines. Very small attachment knob below operculum rostrally. Pair of soft lobes below carinal end of opercular bars, covered with short setae and bearing short spines mostly along free edge (Fig. 1a).

Labral crest with denticles, short setae on surface (Fig. 1c). Mandibles serrate with 2–4 teeth (Fig. 1d, e); inferior angle with 6–12 sharp spines along distal edge; distal part of blade with short hairs and setae. Mandibular palps tapered, twice as long as broad, covered with fine hairs, row of setae along posterodistal edge (Fig. 1f). Superior angle of maxillule (Fig. 1g, h) with 2–3 large spines, 2 smaller ones, then a notch with a few small spines; inferior half of distal margin with numerous medium-sized spines; faces distally setose with proximal field of cuticular ctenae along superior margin. Maxillae triangular, as high as broad, with setae on anterior face and both margins, denser and longer on medial edge (Fig. 1i).

Mouth cirri with long, arcuate coxae; bases a third as long as coxae, twice as long as wide (Fig. 1j, k). Anterior ramus 5-segmented (fifth article often partly or wholly fused to fourth), posterior one 2–4 segmented. Basis and rami armed mostly posteriorly with plumose setae, 2 rows on anterior ramus.

Four pairs of terminal cirri, first shortest, second intermediate, third and fourth longest. Posterior ramus of each (endopod) generally a few articles longer than anterior ramus (exopod). Among 4 specimens examined, segmental counts rarely varied by more than 3. A typical segmental count is as follows (?, repeated counts not equal; +, part of ramus broken off and not counted):

		III	IV	V	VI
Right	Exopod	20	33	40	46
	Endopod	28	33+	42	52
Left	Exopod	21	34	44	43?
	Endopod	28	39	48	49+

Medial setae on coxa and basis. Five setae on anterior side of each cirral article (Fig. 1l): 3 distal (long, medium long, very short), 2 unequal short ones at midlength, at each position the most lateral seta longest. Long distal seta on posterior margin of each article in first pair (III), every 2–3 articles in others; single short seta at longer intervals, and then usually coincident with a long one.

Caudal appendages 2-segmented, not including basal pedestal, reaching to midlength of protopod of last cirrus (Fig. 1m); second article longer than first or pedestal. Tuft of about 7 plumose, distal setae on second article, 2–3 on first.

Males: Attached to mantle or to edge of rostrum of 2 different females. One with pear-shaped body 0.44 mm long, 0.32 mm high (Fig. 1n). Cuticle at narrow end with circular striations. Pair of antennules rising directly from body at lower corner of thick end. Other male V-shaped, 0.5 mm wide, larger arm 0.6 mm long; antennules rising from long, tapered, anteroventral protrusion (Fig. 1o). Antennules in both specimens 4-segmented, first article short, second elongate, third slightly flared distally for attachment, fourth a small appendix of the third.

Burrows. —Corals with burrows were of varying states (Table 2). A few were alive when collected, as shown by the brown remains of dried tissue. Most were recently dead, lacking tissue, but still white and little eroded. One, with an extensively pitted surface and dark deposits of mineral precipitates, had clearly been dead for some time. The majority of the burrows occur on the surface of the coral opposite that bearing the calices.

Burrow apertures are key-hole shaped, 0.8–2.5 mm long, and 0.2–1.0 mm wide (Fig. 2). The carinal end is rounded, while the rostral end tapers to a constriction formed by a protruding shelf of cement and the end of the rostrum. There is often a light-

TABLE 2. *Enallopsammia amphelioides* (Alcock) [? = *E. rostrata* (Pourtalés) of the Atlantic; cf. Cairns 1982] branches from Hawaii containing burrows of *Lithoglyptes viatrix* new species. Coral condition when collected: 1, alive, brown; 2, recently dead, white, costae rough; 3, white, costae smooth; 4, white, costae obliterated, or minor pitting; 5, long dead, grey, considerable pitting. For burrow number, the first entry is the number of burrows unambiguously assignable to *L. viatrix,* the entry in parentheses is the number of other possible acrothoracican burrows (usually very small) of unconfirmed origin.

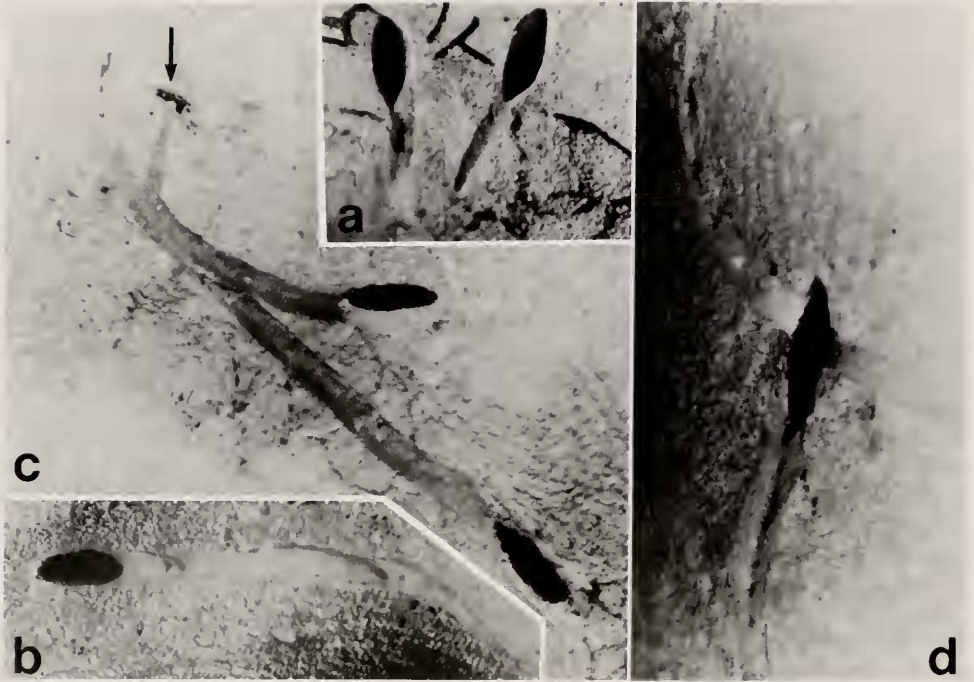| Collection	Coral condition	Burrow number	Burrow condition
R. Grigg, *Sango* III, Kaena Pt., Oahu, 9-VIII-1970, 21°35'N, 158°24–25'W, 440–490 m	5	10	Empty
	3	5	Empty, collapsed
R. Grigg, *Sango* III, Kaena Pt., Oahu, 9-VIII-1970, 21°35.8'N, 158°24.3–24.9'W, 470–475 m	2	5	Empty, except 1 with an opercular bar
	1	2	Empty
R. Grigg, Kaena Pt., Oahu, 19-XII-1973, 378 m	1	16	5 occupied
R. Grigg, *Sango* XIII, Kaula Rock, 30-VIII-1971, 21°43.0–43.8'N, 160°36.5–37.5'W, 386–500 m	3	5	Empty
	4	24 (1)	1 occupied
	3	25 (1)	4 occupied
T. Chamberlain, Hawaii (Grigg, *personal communication*; Makapuu Pt., Oahu, ~400 m, 1967)	4	22 (6)	11 occupied
R. Grigg, *Sango* XIII, Brooks Banks, 23-VIII-1971, 24°0.9'N, 166°42.5'W, 384–432 m	2	0 (1)	Empty
	4	8	Empty
	3	1	Empty
	4	13	1 occupied
	4	7	Empty
	1	1	Occupied

FIGURE 2. Burrows and trails of *Lithoglyptes viatrix* new species on *Enallopsammia amphelioides*. a, Typical burrows with short trails (most examples no longer than this); b, Burrow with long trail; c, Two long trails, the younger one having partly incised the older, arrow pointing to aperture of burrow of unknown origin (possibly acrothoracican or polychaete); d, Two long trails, younger barnacle having cut completely through older burrow and trail. Apertures between 1.25 and 2.0 mm long.

colored streak or trail formed by the cement and rostrum extending across the coral surface. The burrows themselves vary from a typical acrothoracican pit to an elongate trench roofed over by such a trail.

Figure 3 shows the distribution of trail lengths on several pieces of coral and compares them with the size of the corresponding burrow apertures. There is no evident correlation. Most trails are only a few mm long (Fig. 2a), but some are as long as 2 cm, and a number of barnacles, including all those burrowing in calices, seem to have no trails at all. The exposed surface of a trail has more or less parallel sides as far apart as the aperture width, but the trail narrows at its extremity. It is generally flush with the coral surface, with arcuate or chevron-shaped, transverse ridges concave toward the aperture (Fig. 2b, d). These ridges are growth lines; they penetrate sharply into the trail, then turn away from the aperture.

Although there are some exceptions, most trails are oriented more or less longitudinally on the coral and, thus, are generally parallel to each other. In some cases one trail partly overlaps another, or begins in the middle of another (Fig. 2c); the original trail in such cases is the one partly excised by the other. A burrow aperture may also cut into an established trail (Fig. 2d), but no trails were observed to cut all the way across another. A burrow can be straight, or it can twist and turn vagariously in three dimensions. It is usually curved at least a little (Fig. 2c, d) and may even "bank" as it bends around an obstruction like a calice or pit. Trails, at least their older portions, are occasionally overgrown by the host coral. In cross-section or at a break in the coral, burrow roof material can be seen under a layer of coral skeleton. In other cases, the burrow roof is collapsed, leaving a deep trench in the coral; no collapsed burrow was occupied by a barnacle. In one piece of coral, the trails were recessed into trenches but not overgrown. Two of these recessed trials "sideswiped" each other at different levels below the coral surface.
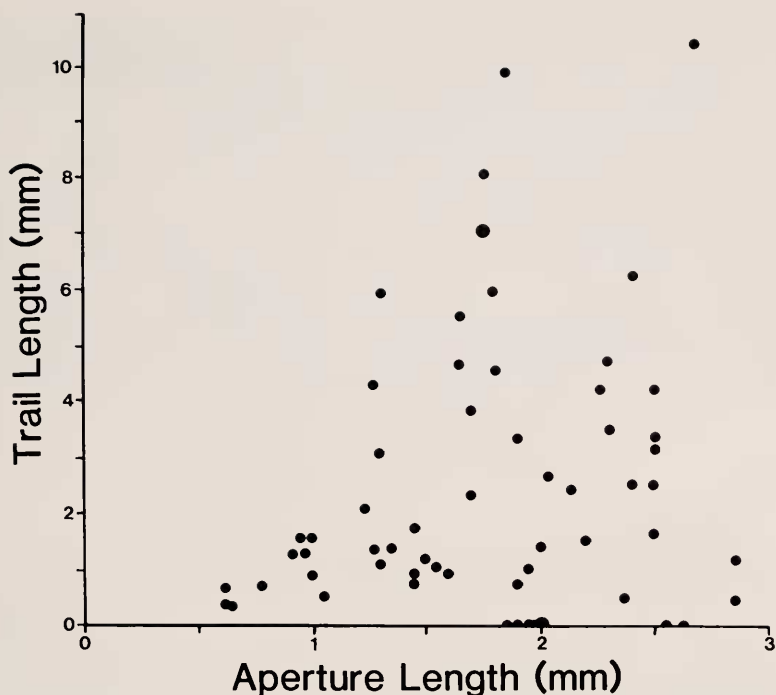
FIGURE 3.   Relationship of aperture length to trail length for the type lots of *Lithoglyptes viatrix* new species burrowing in *Enallopsammia amphelioides*. Only trails whose extremities are clearly visible are included; larger dots are superimposed records.

   A typical elongate, horizontal trail is composed of a rostral plate and the cement holding it in place. This compound structure overlies a horizontal burrow with an elliptical cross-section higher than wide (Fig. 4a, b). The convex top of the rostrum is not exposed because of overlying cement. In the rostrum's thickest, central part, several upwardly convex layers corresponding to growth increments are visible. A thin layer of cement or cemented tailings lines the sides and bottom of the burrow.
   The rostrum is bounded by a chitinous membrane which remains after acid dis-solution. This chitinous structure retains the shape of the rostrum and exhibits obvious growth lines. It has a large open end attached to the edges of the extensive, calcium carbonate-secreting region on the rostral side of the barnacle's mantle (Fig. 4c–f).
   The cross-section of the trail (Fig. 4b) also shows how the rostrum is held within the top of a parallel-sided trench above the burrow lumen by an organo-calcareous cement (white by reflected light, orange-brown by transmitted) that adheres to the coral and to the chitinous lining of the upper lining of the rostrum. This cement, which may not be entirely of secretory origin (Kamens 1981), must be laid down by a different mantle region than the rostrum-secreting area, likely on the rostral side of the short neck below the opercular bars.
   When subjected to acid, the cement dissolves much more quickly than the rostrum, at least in part because of the thin chitinous membrane separating the two. When the thin layer of cement covering the upper side of the rostrum is fully dissolved, this membrane is evident, and the two calcareous structures are quite distinct. The cement is a very bright, opaque white, whereas the rostrum is lustrous and translucent, but uncolored, and appears much less bright.
   Comparison. —The 4 pairs of terminal cirri and the caudal appendages are diag-nostic of *Lithoglyptes* (Tomlinson 1969). Most of the species in this genus have prom-inent hooks on the operculum and, therefore, can be readily distinguished from *L. viatrix.* Those that do not have hooks are *L. indicus* Aurivillius, *L. mitis* Tomlinson,
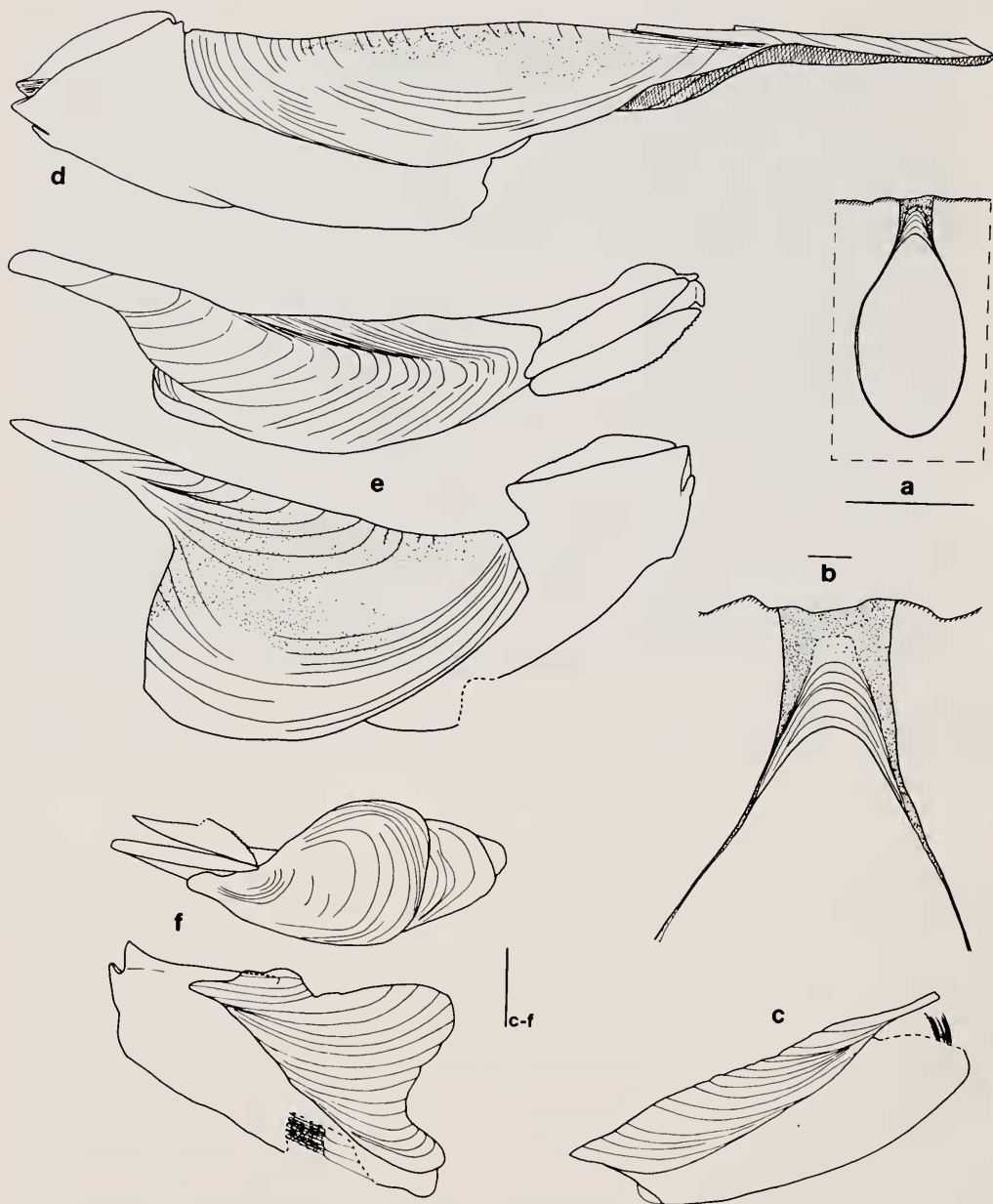
FIGURE 4. *Lithoglyptes viatrix* new species, burrow structure and rostral growth. a, Cross-section of burrow (coral surface hatched, calcareous cement stippled, rostrum with growth lines); b, Detail of burrow roof in a. c–f, Adult females dissolved out of coral substrate; remaining calcareous part of rostrum stippled. c, Primitive rostral growth, new layers added away from aperture (precise orientation in coral unclear and operculum lost); d, Advanced rostral growth, new layers added at apertural end, resulting in bodily translation; e, Rostral and side views of specimen that initially grew as in d, but stopped moving and grew in place; f, Rostral and side views of specimen that grew like older stage of e, but was obstructed away from the aperture by an overgrown thoracican barnacle. Scale bars 1 mm except 0.1 mm in b.

and some specimens of *L. habei* (Tomlinson). The last two have bifid rather than simple opercular spines and teeth. *Lithoglyptes indicus* has many small spines rather than scattered papillae over the faces of the opercular bars. It also has elongate rather than short distal articles on the caudal appendages, and the rostral side of the mantle is at

an angle to the operculum rather than being parallel. The significance of a calcareous rostrum, not previously known to occur in this genus, is considered in the Discussion.

Associated fauna. —Some empty burrows are secondarily inhabited by a tanaid. One barnacle-occupied burrow had its aperture covered by a sponge. About a dozen very small burrows were interspersed among those of *L. viatrix* (Table 2; Fig. 2c). Their apertures are elliptical, typically with a constriction in the middle. Perhaps they were formed by young *L. viatrix* or by spionid polychaetes, but because none was occupied this cannot be demonstrated. A number of corals had old, empty galls of an as yet undiscovered ascothoracid crustacean, presumably a *Petrarca* species; large, round, porous galls are typical of that genus, which has been found infesting *Enallopsammia* in the Atlantic, Pacific and Indian Oceans (Lopez 1974, Zibrowius 1980, Grygier 1981 and in press, Zibrowius and Grygier, in prep.). The corals were often fouled with bryozoans, foraminiferans, gammaridean amphipods, and juvenile balanomorph barnacles [*Chionelasmus darwini* (Pilsbry); Newman, in prep.].

Lithoglyptes tectoscrobis new species
Figure 5

Diagnosis. —The calcareous cement and rostrum form a roof over an elongate trench-like burrow. The mantle is elongate with a tubular distal end, and the carinal margin is broadly rounded. The first terminal cirrus (III) has an exopod longer than the endopod.

Material. —Holotype female (USNM 210848) in *Enallopsammia amphelioides* (=? *E. rostrata*; *see* Cairns 1982) collected by Committee for the Coordination of Joint Prospecting for Mineral Resources in South Pacific Offshore Areas (CCOP/SOPAC), Tonga Offshore Survey Stat. 78(2)-5, 12-XI-1978, 19°25.0'S, 174°13.4'W, 250–290 m; forwarded by R. W. Grigg.

Etymology. —From Latin *tectum* (roof) and *scrobis* (trench), referring to the roofed burrow.

Description. —Mantle 5.7 mm long, aside from a narrow, 1.0 mm long tube at rear; semicircular in side view, 1.7 mm across at midlength; operculum parallel to rostral side of mantle (Fig. 5a, b). Operculum 1.9 mm long, 0.7 mm across, carinal end rounded, rostral end distinctly tapered (Fig. 5c, d). Lateral edges with irregular denticles and short, fine hairs; faces with numerous, regularly spaced papillae interspersed among and dotted with innumerable granules; medial edges with no special armament, but papillae a little more abundant there. Mantle set with simple, bifid, or trifid spinules, proximal part also with fine hairs, larger and more abundant toward carinal end. Comb collar between opercular bars. Pair of small lobes below carinal end of operculum, thickly set with hairs and bearing about 15 strong teeth each. Long setae on inner mantle wall near operculum, denser toward carinal end. Attachment knob inconspicuous, focus of radial array of mantle muscles; prominent longitudinal muscles also present. Rostral surface largely an oval, yellow, glandular region. Tube rising from near back end of this tissue, with proximal half hollow and distal half plugged with several layers of chitin (Fig. 5e).

Row of conical denticles along crest of labrum (Fig. 5f). Mandibles with 3 narrow teeth separated by deep notches (Fig. 5g, h); inferior angle with 7–8 small teeth and large, trifid tooth at very tip; setation as in *L. viatrix*. Mandibular palps tall, narrow triangles with posterior row of setae (Fig. 5i). Maxillules as in *L. viatrix*, but spines near inferior angle smaller than rest (Fig. 5j). Maxillae a little longer than broad, broadly pointed, with row of setae along distal margins and other setae scattered over distal half of anterior face (Fig. 5k).

Bases of mouth cirri half as long as coxae; anterior ramus 5-segmented, posterior one 3–4-segmented (Fig. 5l). Setation similar to *L. viatrix*.

Four pairs of terminal cirri. First pair shortest, second next shortest, last 2 pairs equally long. Segmental count of exopod larger than endopod in first pair, reverse in
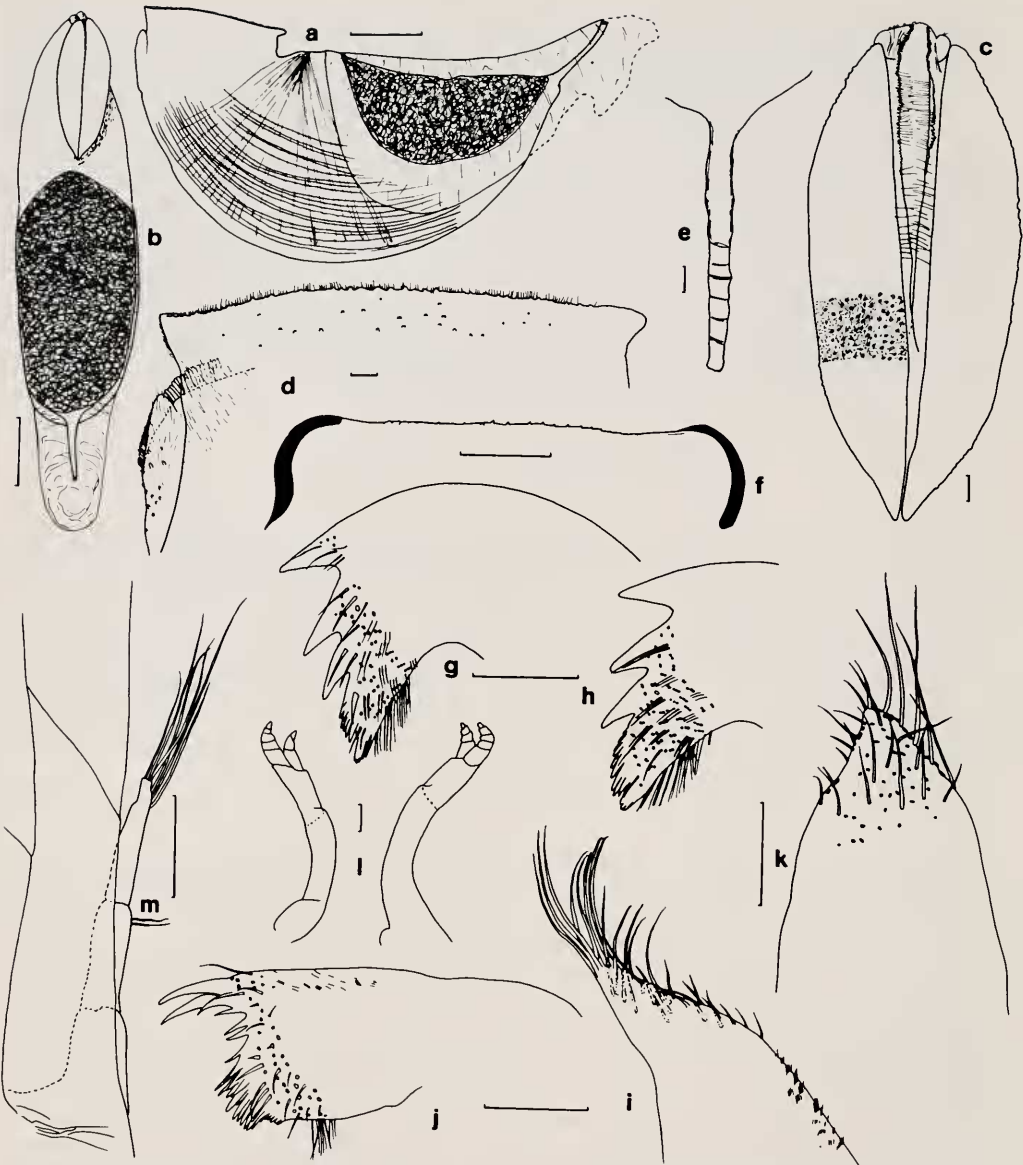
FIGURE 5. *Lithoglyptes tectoscrobis* new species, holotype female. a, b, Lateral and rostral views of whole animal, shaded region glandular, chitinous rostral lining present (calcareous part dissolved away); c, d, Operculum, top and side views, papillae and granules shown only for part of one valve; e, Posterior mantle tube; f, Labral crest, flattened out; g, h, Mandibular gnathobases, only insertion sites shown of many setae; i, Mandibular palp; j, Maxillular gnathobase; k, Maxilla, front view; l, Mouth cirri (I), setae omitted; m, Protopod of last cirrus (VI) and caudal appendage. Scale bars 0.1 mm except 1 mm in a and b.

second pair, almost equal in third and fourth pairs. Setation as in *L. viatrix*. Segmental counts as follows:

		III	IV	V	VI
Right	Exopod	37	42	55	55
	Endopod	28	50	55	57
Left	Exopod	36	44	51	55
	Endopod	26	50	54	56

Caudal appendages 2-segmented, on pedestal, reaching to midlength of protopod of last cirrus (Fig. 5m). Basal article little longer than pedestal, with 2 posterior, subterminal setae; distal article little longer than basal one, with 6 terminal setae.

Eggs. —Oblong mass of about 1200 yellow, oval (0.18 × 0.13 mm) eggs in mantle cavity, number estimated volumetrically.

Gut contents. —Apparently of detrital origin, including sponge spicules, yellow-green globules, a few possible crustacean parts, and large quantities of a granular, amorphous substance.

Burrow. —Aperture 1.95 mm long, 0.70 mm wide, a tapered oval narrower at rostral end. Trail 3.9 mm long, identical in external appearance to those of *L. viatrix.* Aside from proximal and distal ends, trial overgrown by coral skeleton. Barnacle occupying all except innermost part of burrow, where mantle tube continues up and out toward coral surface.

Comparison. —The only acrothoracican comparable to *L. tectoscrobis* is *L. viatrix,* with which it shares a major specialization—the rostrum employed as a burrow roof (*see* Discussion). It differs from *L. viatrix* in having a tube at the end of the mantle, even less opercular armament, smaller lobes below the carinal end of the operculum, and a longer exopod than endopod on the first terminal cirrus. This last character is highly unusual; all other species of *Lithoglyptes, Weltneria,* and *Berndtia* have a longer endopod than exopod on the homologous limb (III; second terminal cirrus in the last 2 genera) (Tomlinson 1969), although limb II, when present, may have a longer exopod (cf. *W. ligamenta* new species below).

Weltneria Berndt, 1907

Diagnosis. —Lithoglyptids with 5 pairs of terminal cirri (II–VI) and a pair of caudal appendages (Table 1).

Weltneria ligamenta new species
Figure 6

Diagnosis. —Opercular bars are connected by a conspicuous, bipartite "ligament." No setae or marginal teeth are present on opercular bars.

Material. —Holotype female (USNM 210846) from same collection as *lithoglyptes tectoscrobis* new species.

Etymology. —From Latin *ligamentum* (a band or tie), referring to the remarkably well-developed ligament connecting the opercular bars.

Description. —Typical, sac-like mantle. Operculum 2.7 mm long, 0.6 mm across at widest point (about ⅓ of way from rostral end); bars connected there by pair of elevated, oval longitudinally aligned, medially fused "ligaments" one-fourth as long as bars (Fig. 6a, b). Opercular armament feeble, numerous small papillae scattered over faces and margins, no apical hooks. Carinal half of medial margins crenulate, paralleled internally by comb collar. Mantle wall below operculum scaly, with small papillae; heavier spines along carinal edge.

Bullate labrum with curved setae on each side, crest with evenly spaced denticles (Fig. 6c). One mandible serrate, with 4 teeth, other with 5 (Fig. 6d, e); inferior angle with 2–4 heavy spines; faces sparsely covered with setae, inferior margin with long, fine hairs. Triangular mandibular palps flanking labrum, about twice as long as wide, with setae along posterior edge, few distal setae along edge (Fig. 6d). Maxillules with strong spine at superior corner, about 10 lesser spines in 3 loose clusters along cutting edge; faces with few strong, distal setae, distal part of inferior margin with many long, fine setae (Fig. 6f, g). Maxillae joined basally, longer than broad with blunt tips; abundant setae along distal margin and down anterior face (Fig. 6h).

One mouth cirrus lost in dissection. Other well-developed, with long, curved coxa (possibly secondarily jointed at about ⅓ length), short setose basis (Fig. 6i); anterior ramus 6-segmented, each article well-armed with setae; posterior ramus 3-segmented, first article longest, all setose (Fig. 6j).

Five pairs of terminal cirri. First shorter than others, exopod much longer than endopod. Other cirri progressively longer, exopods slightly shorter than endopods. Setation as in *L. viatrix* (Fig. 6k). Segmental counts ±1 (2 counts) as follows:

		II	III	IV	V	VI
Right	Exopod	21	31	43	51	52+
	Endopod	14	38	49	53+	54+
Left	Exopod	22	32	41+	48	52
	Endopod	15	39	47	54	57+

Caudal appendages biarticulate, half as long as coxa of last cirrus, each article with heavy terminal setation (Fig. 6l).

Burrow. —Coral broken at burrow and portion bearing rostral half of burrow lost, so existence of calcareous rostrum unverifiable; carinal end of aperture round.

Comparison. —*Weltneria ligamenta* fits the diagnosis of the genus given by Tomlinson (1969) in having 5 pairs of terminal cirri and caudal appendages. It differs from the 6 previously described species in the unique development of an opercular "ligament" and in the lack of setae and marginal teeth on the operculum.

<center>

Weltneria griggi new species
Figure 7

</center>

Diagnosis. —A calcareous rostrum is present. The opercular bars have abundant long setae, simple spines along the lateral edges, papillae along the medial edges, and more complex spines laterally on the faces.

Material. —Holotype female (USNM 210847), dried. Collected 22-I-1972, R/V *Oregon* Sta. 11722, 31°46′N, 79°15′W (vicinity of Blake Plateau), 402 m, in *Enallopsammia rostrata*.

Etymology. —Named for R. W. Grigg (Hawaii Institute of Marine Biology), in appreciation for amassing the coral collections in which most of the material described herein was discovered.

Description. —Mantle a simple sac 5.8 × 3.6 mm (Fig. 7a). Longitudinal musculature clearly evident. Small papillae and bifid or trifid spinules scattered about (Fig. 7b), and sub-opercular region with hairs, more extensive along carinal side. Rostrally upswept opercular bars 2.5 mm long, each 0.43 mm across just rostrad of midlength (Fig. 7c, d). Rostral half generally wider than carinal half, but tips equally sharp. Long setae on faces and along lateral edge, short setae along medial edge. Sharp spines along lateral edge, blunt papillae along medial edge. Smaller papillae on medial half of face; tall, simple or bifid spines on lateral half. Comb collar present. Thorax bent into the shape of an S within mantle (Fig. 7e).

Bullate labrum with cuticular ctenae and lateral setae; crest with row of blunt denticles (Fig. 7f). Mandibles with 3 teeth, inferior angle blunt or divided into several small teeth, setation heavy, but absent on superior tooth (Fig. 7g, h); mandibular palps narrow with many setae distally and posteriorly (Fig. 7g). Maxillules with 2 large and 2 small superior teeth, a gap, and about 10 inferior teeth; setation typical (Fig. 7i, j). Maxillae broad, triangular, with row of long, medial setae, as well as shorter anterior and lateral setae (Fig. 7k).

Mouth cirri with long, slightly arched coxae and short, non-setose bases (Fig. 7l). Anterior ramus with 4 segments in one, 3 in other, posterior with 5 segments in both, and setation essentially the same in both despite different segment number (Fig. 7m).

Five pairs of terminal cirri. Cirral articles armed as in *L. viatrix*. First cirrus shortest, second next longer, other 3 pairs about same length, exopods apparently shorter than endopods, but not confirmed in all limbs (many broken off); segmental counts as follows:

		II	III	IV	V	VI
Right	Exopod	?	30	?	38	39
	Endopod	?	?	41	46	48
Left	Exopod	?	31	?	?	47
	Endopod	20	36	43	45	46

FIGURE 6. *Weltneria ligamenta* new species, holotype female. a, b, Lateral and top views of operculum, ligament shaded (arrow); c, Labrum and mandibular palps, rear view; d, e, Mandibular gnathobases, d with palp, only some setae shown in full, setae omitted from e; f, g, Maxillular gnathobases, setae not shown in full in f, omitted in g; h, Maxillae, rear view; i, Mouth cirrus (I), arrow pointing to possible secondary joint in coxa (or break); j, Rami of i; k, Typical setation of middle part of terminal cirrus (III–VI); l, Caudal appendage (removed from pedestal). Scale bars 0.1 mm except 1 mm in a and b.

FIGURE 7. *Weltneria griggi* new species, holotype female. a, Whole animal, lateral view, cuticle of rostrum shown, remaining part of rostrum stippled; b, Types of mantle spines; c, d, Lateral and top view of an opercular valve; e, Cutaway view of mantle, showing folded thorax and terminal cirri; f, Labrum, side view; g, Mandibular gnathobase and mandibular palp; h, Inferior angle of other mandible; i, j, Maxillular gnatho- bases, setae omitted in j; k, Maxilla; l, Mouth cirrus (I), some muscles shown; m, Rami of l, most setae only shown as bases; n, Protopod of last terminal cirrus (VI) and caudal appendage; o, Detail of caudal appendage in n. Scale bars 0.1 mm except 1 mm in a and e.

Caudal appendages 2-segmented, less than half as long as coxa of last cirrus (Fig. 7n, o); articles equal, first with 2–3 anterior setae, second with 1 short, several long, plumose setae.

Burrow. — Aperture 2.5 × 1.2 mm; 0.65 mm of trail visible on coral surface.

Comparison. — The 5 pairs of terminal cirri and caudal appendages assign this specimen to *Weltneria* (Tomlinson 1969). Like *W. hessleri* Newman, and *W. exargilla*

Newman, *W. griggi* lives in deep water and has a calcareous rostrum. However, this plate has a different shape and orientation, being transitional towards those of *Lithoglyptes viatrix* and *L. tectoscrobis* (*see* Discussion). The opercular armament differs from both of the earlier rostrate species of *Weltneria,* and there are fewer articles on the rami of the mouth cirri. *Weltneria griggi* differs from *W. spinosa* Berndt in lacking a pair of opercular hooks, and from that species and the remaining three, *W. hirsuta* (Tomlinson), *W. reticulata* Tomlinson, and *W. aapta* Tomlinson, in having only simple, not bifid, lateral opercular spines. Unlike *W. ligamenta, W. griggi* has no "ligament" joining its much more heavily armed opercular bars.

<center>DISCUSSION</center>

The Rostrum and Motility in Lithoglyptes viatrix

Weltneria hessleri and *W. exargilla,* North Atlantic abyssal inhabitants of calcareous and muddy bottoms, respectively, were the first acrothoracicans found to have a calcareous rostrum (Newman 1971, 1974). Their rostrum is a triangular plate, much like that of scalpelloid barnacles, but it is cemented to the burrow wall (Fig. 8, Ia). The umbo is apical and projects freely; successive growth increments are added at the bottom edge as the animal burrows deeper into the substrate. Turquier (1978) disputed that this plate is homologous with the scalpelloid rostrum because he inferred that its position was not "rostral." Newman (1982) refuted the objection; the plate is rostral in form and position, but its homology with the rostrum of ordinary barnacles can, without additional evidence, always be doubted. In any event, it is a structural feature of these acrothoracicans, distinct from secreted, calcified cement.

Newman (1974) pointed out that the so-called cement discs, composed of uncalcified cement and exuvia, and which anchor most acrothoracicans within their burrows, sometimes have a rostrum-like appearance (*see* examples in Tomlinson 1969). It is not possible to tell from wholly decalcified specimens (the usual technique for extracting the barnacles) whether a rostrum or just a cement disc was involved. However, there are two ways to tell the difference in untreated specimens. If two distinct sorts of material are exposed, either in section or by partial dissolution, as in *L. viatrix,* it is likely that one is the rostrum and the other the cement holding it in place. We urge future investigators to examine at least some burrows mechanically before acid dissolution in order to verify the presence or absence of a rostrum. For example, we so treated *Lithoglyptes spinatus* and found no rostrum, just cement. The calcareous shield in the burrows of *Lithoglyptes indicus* is of calcified cement only and is not a rostrum, since no cuticular lining or other organic trace is left after dissolution in acid (Aurivillius 1894).

The burrows, and especially the rostra, of *L. viatrix* are extremely variable. Sometimes the animal digs into the coral substrate while producing a rostrum with an apical umbo near the operculum, in the same manner as Newman's *Weltneria* species (Fig. 4c). At the other extreme, the burrow and rostrum develop in a horizontal direction, with the umbo at the end farthest from the operculum (Fig. 4d). New growth increments are added at the opercular end and cemented laterally to the burrow walls, forming the longer of the so-called trails described in detail above. The horizontal burrow is apparently excavated by the carinal end of the mantle as newly secreted rostrum and cement advance the animal against the carinal wall of the aperture. The spines on the lobes below the operculum probably play an important role in the abrasion process, likely combined with chemical action (Kamens 1981).

Most *L. viatrix* are intermediate between these two extremes (Fig. 4e, f) in having trails about as long as the burrow apertures. The rostra in such individuals have a variety of forms, revealed upon dissolution, that reflect changes in proportion of the vertical and longitudinal components in growth (growth referring to the addition of increments to the rostrum relative to the surface of the coral). One can assume that the cues regulating this behavior involve orientation to currents, avoidance of burial, interference from neighboring barnacles, obstructions to growth (such as balanomorph
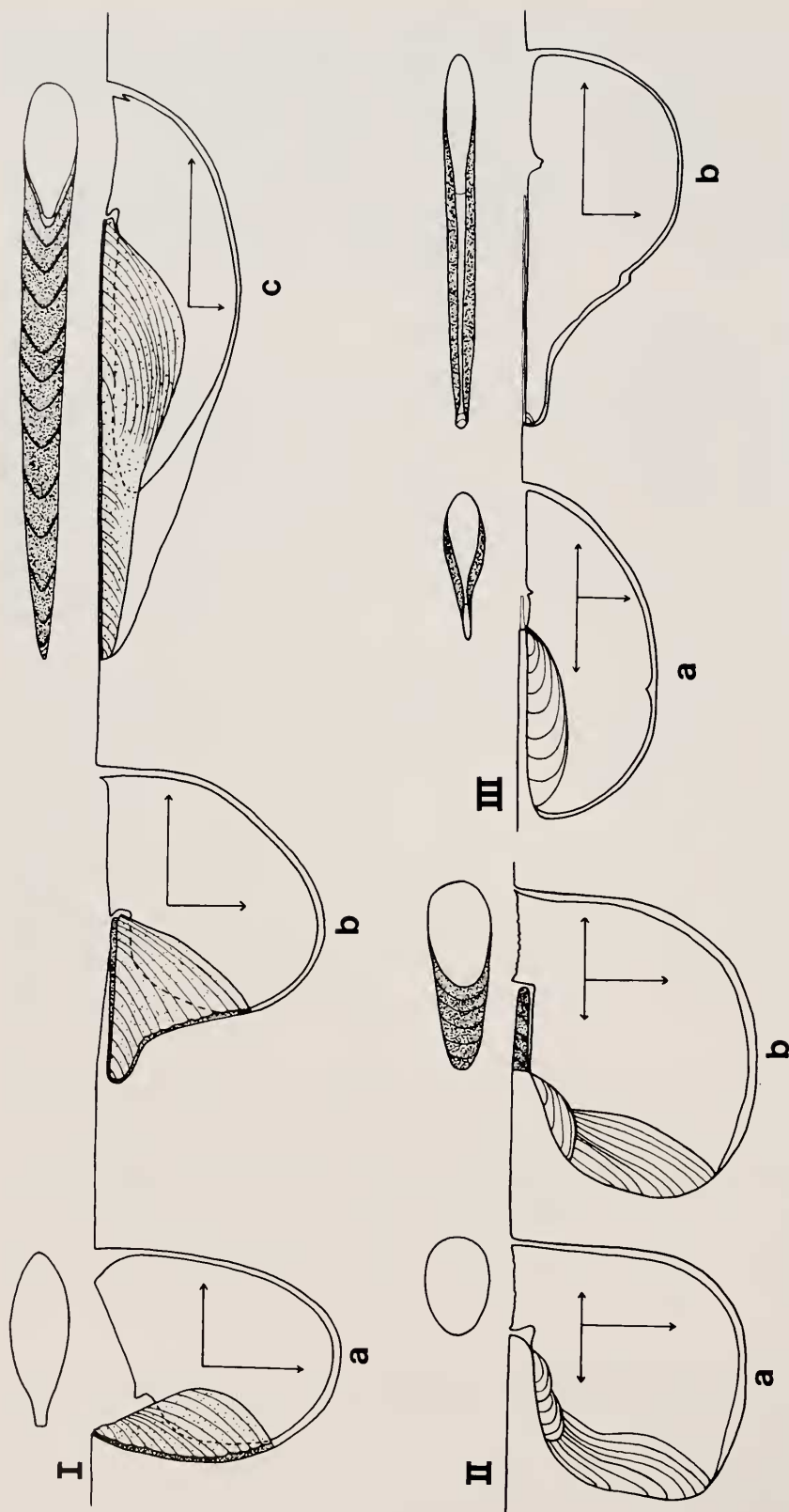
16

FIGURE 8. Calcareous structures, growth, and motility in extant Acrothoracica. I. Lithoglyptidae. a, *Weltneria exargilla* Newman; b, *Weltneria griggi* new species, rostrum partly overgrown by coral; c, *Lithoglyptes viatrix* new species. II. Cryptophialidae. a, *Australophialus utinomii* (after Tomlinson 1969); b, *Australophialus melampygos* (Berndt). III. Trypetesidae. a, *Trypetesa lampas* (Hancock); b, *Trypetesa* species (Standing and Tomlinson, in prep.). All are shown in cutaway lateral view in situ, with external views of the apertures of most of them. Dark stippling is calcareous cement, light stippling is the rostrum, unshaded with growth lines is non-calcareous cement, and unshaded without growth lines in III is a tough membrane. Arrows indicate the longitudinal and vertical components of growth and burrow enlargement.

barnacles and coral calices), etc., but the relative importance of such cues cannot be estimated without experimental evidence.

In cases where burrow excavation proceeds horizontally, the animal does not remain attached at the origin of the burrow, passively growing to occupy newly available space. Rather, the animal is carried along as rostral growth continues, and as a whole abandons the older part of the burrow (Figs. 4d, e; 8, Ic). It may eventually move farther than its body length. If the old burrow were not roofed by the rostrum, the barnacle would be vulnerable to attack from the rear; apparently because of the trail no foreign organisms were ever found in the evacuated part of a barnacle-occupied burrow. Sometimes secondary inhabitants (tanaids, etc.) live in empty burrows. It is unlikely that one burrow successfully crosses another because accidental intrusion into an abandoned burrow invites attacks from predators.

Homologues and Analogues in Extant Forms

Lithoglyptes tectoscrobis has an elongate, horizontal rostrum like some specimens of *L. viatrix*. Since only one specimen was available to us, we cannot say whether this is typical, or if this species shows the same range of growth forms as *L. viatrix*. *Weltneria griggi* has a rostrum that exhibits both vertical and horizontal growth (Fig. 8, Ib). Again, the range of its behavior is not known. *Weltneria hessleri* and *W. exargilla,* the only previously known deep-sea lithoglyptid acrothoracicans, both have more conventional, vertically oriented rostra. One begins to suspect that most large, deep-water acrothoracicans have rostra. *Weltneria ligamenta* may have had one, too, but unfortunately the part of the coral that would have borne it was unavailable for examination. In all the cases so far mentioned, it is certain that the rostra are homologous.

Noll (1875), in his drawings of *Kochlorine hamata* from Cadiz, Spain, shows grooves in the gastropod shell substrate (*Haliotis tuberculata* Linné) leading to burrow apertures. He attributed the grooves to abortive attempts of the newly settled cyprid larvae to begin excavation. Where known, however, the larvae do not begin to burrow until after attachment and metamorphosis (Batham and Tomlinson 1965, Turquier 1970). Therefore, the floor of these grooves is more likely the cement layer over a partly horizontal rostrum, or the rostrum itself. We have as yet been unable to obtain specimens of this species in situ to confirm this suspicion.

All of the foregoing examples have been from the primitive family Lithoglyptidae. This is not surprising. If the rostrum is a holdover from a thoracican barnacle ancestor, its presence is a plesiomorphic condition liable to be maintained in one or more lines of descent.

An analogue to the situation in *L. viatrix* is provided by *Australophialus melampygos,* a representative of the more plesiomorphic genus of the otherwise advanced Cryptophialidae, living in shells such as that of the mussel *Perna canaliculus* Gmelin from New Zealand. Batham and Tomlinson (1965) photographed burrow apertures that had a white streak extending from each of them, which they interpreted as accumulations of tailings (sensu Darwin 1854; *see* below). In reexamining this species, we discovered that the white streak is a cement burrow roof, as in *L. viatrix,* but that there is no rostrum and the mantle is not attached to the roof (Fig. 8, IIb). There is a normal cement disc at the end of the burrow holding the barnacle in place. As the aperture moves, apparently to even out the inter-apertural distances, the mantle expands in the carinal direction, no part of the burrow being evacuated. Some burrowing takes place around the edges of the cement disc, which is eventually replaced by a larger, deeper one. Tomlinson (1969) shows such a series of cement discs in this species and also in *A. utinomii* Tomlinson (Fig. 8, IIa).

Other living analogues are *Trypetesa lampas* (Hancock) of the North Atlantic, described by Darwin (1854) as *Alcippe lampas,* and by an undescribed species of *Trypetesa* from North Carolina (Standing and Tomlinson, in prep.) (Fig. 8, III). The latter settles on the lip of gastropod mollusk shells inhabited by hermit crabs. It then burrows toward the interior, sometimes reorienting 180° before doing so. In many cases the burrow aperture is a normal ellipse, but often there is an additional, narrow, curved

slit from the rostral end. This slit may extend a short distance in *T. lampas,* or several times the length of the opercular part of the aperture in the new species of *Trypetesa* and in some specimens of *T. lateralis.* The edges of the slit in all but the last species are formed of a secreted white substance reminiscent of the cement in *L. viatrix* (Fig. 8, III). Darwin (1854), contrary to Hancock (1849), considered the calcareous rims to be inorganic accumulations, rather than secretions of the animal. Kamens (1981) studied the burrows of *T. lampas* with SEM and chemical tests and showed that the calcareous part of these deposits probably originates from the inhabited gastropod shell as a breakdown product, not as a precipitation of dissolved $CaCO_3$, but as redeposited calcareous spherules. He could not determine the source of the organic matrix, but most acrothoracicans are capable of secreting an uncalcified, organic cement, so we think it likely that such a substance serves as the organic matrix here. The calcified cement of other acrothoracicans, including *L. viatrix,* may have a similar compound origin. We did not observe lines of deposition noted by Darwin (1854) and Kamens (1981), but the exposed surfaces were generally worn flush with the surface of the snail shell and, therefore, the lines of deposition may have been abraded away by the actions of the hermit crab.

Trypetesa is weakly attached within the burrow. In *T. lampas* this is accomplished by a disc-like mantle expansion (Fig. 8, IIIa), and very weakly if at all in the undescribed species by the tip of a long, prow-shaped mantle projection (peduncular rudiment) (Fig. 8, IIIb). The slit itself is closed by a thin, tough, membranous material in both species, and there is no rostrum.

Fossil Acrothoracica with Roofed Burrows

Zapfe (1936) described and provided photographs of Miocene acrothoracican burrows in the gastropods *Pyrula cornuta* Agassiz (apertural view of shell and an enlargement of a region of same) and *Fasciolaria tarbelliana* Grateloup (apertural view of shell). The same two photographs of *Pyrula* were published by Häntzschel (1962:W231; fig. 144, 1a and b, and 1975:35; fig. 83, 2c and d) as borings of the ichnogenus *Zapfella* in the gastropod *Galeodes* (*Volema*) *cornuta* from the lower Miocene of Hungary. The photographs of *Galeodes* show grooves leading away from the narrow end of the aperture in several cases, much like Noll's (1875) drawing of *Kochlorine hamata* discussed above. Saint-Seine (1954) apparently considered these specimens specifically distinct from her *Zapfella pattei,* but in that genus. We could not examine that specimen because it was destroyed in World War II (F. F. Steininger, *personal communication*), but we were able to obtain the infested shell of *F. tarbelliana* (IPUW-2522/84). Three of its burrows have a short, *L. viatrix*-like trail with a few chevrons (growth lines) on the surface of a sunken roof (rostrum?) and apparently cement on the walls of the trench above the suspected rostrum. It seems that much of the rostrum and some of the cement had been eroded away. This is the best candidate for a fossil homologue of the *L. viatrix* rostrum system. Although more study is required, Zapfe's specimens most likely represent primitive lithoglyptids, but from shallow rather than deep water.

Other fossil analogues of the *L. viatrix* system, perhaps homologous with the *Trypetesa* system, are represented by *Rogerella* Saint-Seine (*see* especially Codez and Saint-Seine 1958) of the Mesozoic and Tertiary. *Rogerella* has one end of the burrow aperture wider than the other, and the narrow end produced to a greater or lesser extent into a "peduncular slit" lined on one or both sides with a "bourrelet" of calcareous lamellae, seldom well-preserved. Although originally limited to burrows in echinoid tests (Saint-Seine 1951, 1956), this genus was later broadened to include similar burrows in all sorts of substrates (Codez and Saint-Seine 1958), and now 4 species have been named (*see* also Schlaudt and Young 1960, Voigt 1967).

In *Rogerella lecointrei* Saint-Seine, the bourrelets (one or a pair) are raised above the surface of the sea urchin test, and the calcareous lamellae are oblique, their medial edges pointing away from the main part of the aperture. The bourrelets are apparently continuous with a calcareous lining of the burrow, which becomes thinner and may disappear toward the burrow floor. If they were continuous across the peduncular slit,

which was never observed to be the case in these fossils, the bourrelets would resemble the chevron-incised trails of *L. viatrix*. If never closed over, then the bourrelets are like the calcareous rims in *Trypetesa* species.

In *Rogerella mathieui* Saint-Seine the bourrelets are much more fragile and are very easily lost to erosion, due to the burrow widening suddenly below them. Its burrow is reported to be very deep beneath the entire opercular slit. The bourrelets are rarely preserved in the remaining 2 species, but Voigt (1967) notes that the narrow part of the aperture in *R. caudata* Voigt, which is often bent at a sharp angle to the rest of the aperture, is bounded on both sides by barnacle-secreted, calcareous deposits. Unlike *R. lecointrei,* these bourrelets are sunk into the surface of the host oyster, not raised above it.

We propose that *Rogerella* bourrelets are of calcified cement laid down by the barnacle. The question remains as to whether the peduncular slit is natural or an artifact. A long burrow like that of *L. viatrix* would be similar to those of *R. lecointrei* if the former were moderately eroded to remove superficial cement and the rostrum itself removed by differential erosion, solution, or simple mechanical loss (the last being possible because the rostrum is separated from the cement by a chitinous cuticle). However, well-preserved specimens of *R. lecointrei* exist that show no sign of substrate erosion (Saint-Seine 1951). Although the burrow shape is unknown in *R. lecointrei,* the very deep burrow of *R. mathieui* is quite unlike the long burrows of *L. viatrix,* which are not very deep, and become shallower away from the aperture.

It may be more reasonable to assume that the burrows of *Rogerella* were produced by something akin to the *Trypetesa* species discussed above; the peduncular slit may be a real opening, not a product of surface erosion or rostrum loss. Saint-Seine's descriptive reconstruction of the *Rogerella* barnacle (Codez and Saint-Seine 1958) includes a "peduncle" attached at the end of the slit, supposedly the original larval attachment site. The slit had formed as the operculum moved away from the attachment site, and the lengthening peduncle was partly roofed over and protected by secreted bourrelets (calcareous cement). As in *A. melampygos,* the attachment site is fixed and no bodily translation occurred, just growth. The French authors cite Tomlinson's (1955) description of *Trypetesa lateralis* in support of this model, noting the horny attachment knob borne on a stalk (or "peduncle") longer than usual in the Acrothoracica. The undescribed species of *Trypetesa* from North Carolina, with its very large, distally anchored peduncular rudiment and cement secretions narrowing the open slit above it, is an almost exact analogue to *Rogerella*. A close phylogenetic relationship between the two genera cannot be discounted.

Nomenclatural Significance of Fossil Acrothoracican Hard Parts

As a matter of interest to paleontologists, fossil acrothoracican burrows are ichnofossils (Häntzschel 1975), but the calcareous structures associated with them are sometimes body fossils. A rostrum (which may be present in Zapfe's 1936 specimens) is part of the barnacle's body, although structures composed entirely of mineralized cement (as we suspect for *Rogerella*'s bourrelets) are not. The significance of this distinction is that the International Code of Zoological Nomenclature, Third Edition (Art. 23, g, iii) treats the names of ichnofossils differently from body fossils with regard to the Principle of Priority. It will be necessary in future paleontological studies of acrothoracicans to make explicit whether new taxa are ichnotaxa or not.

Strategies of Motility

Acrothoracicans have several different means of attaching themselves within their burrows, and most of them have a limited capacity for motility after settling. Motility is best defined functionally as displacement of the burrow aperture across its substrate; this may involve growth, bodily translation, or both. Various combinations of attachment mechanisms and growth patterns form coherent sequences of intermediate stages from the primitive condition exemplified by *Weltneria hessleri* and *W. exargilla.*

There are three kinds of extra-mantle structures. A rostrum is a calcareous body

plate firmly attached to the mantle and invested in a chitinous cuticle. There is also mineralized cement, either anchoring the rostrum or the mantle in place, and/or serving a protective function. Most non-rostrate acrothoracicans attach themselves to the burrow wall by a secreted, non-calcareous cement disc that incorporates successively larger parts of the exuvia at each molt (known exception: *Lithoglyptes indicus* with a calcareous cement disc). Mineralized and organic cement may be produced by different parts of the mantle in the same species, but often only one or the other is present.

Our conception of the sequential alterations from a primitive, immotile acrothoracican with a vertical rostrum held in place by mineralized cement (e.g., *Weltneria exargilla*), presently confirmed only in bathyal and abyssal forms, is shown in Figure 8. One strategy is to retain the rostrum and mineralized cement, but to add a horizontal component to rostral growth. This keeps the mantle protected by a hard cover as the aperture moves small distances (e.g., *Weltneria griggi*). The selective advantages of motility, allowing resituation of the mantle opening if the original settling site proved unfavorable, led to a rotation of the mantle so it could remain attached to the under side of a horizontal rostral burrow roof. *Lithoglyptes tectoscrobis* retains a narrow connection to the older end of the burrow (its mantle tube). *Lithoglyptes viatrix* has lost even this connection, making it the first and only truly motile acrothoracican known.

Another highly successful strategy in shallow seas was to lose the rostrum. *Lithoglyptes indicus,* with its attachment disc of calcareous cement, may illustrate an early stage in this process. In all other cases known, the calcareous component of the cement stopped being incorporated, at least in the cement disc. However, mineralized cement is still produced near the operculum in some forms where it has been convergently adopted as a roofing material for a shifting aperture [*Australophialus melampygos, Trypetesa* (point already made for *T. lampas* by Kamens 1981), and *Rogerella*]. All such species rely on mantle growth to force the aperture along. In some cases (*A. melampygos, T. lampas*) the distal end of the mantle is broadly stuck to the burrow wall so the animals cannot move. Their capacity to reposition themselves is more limited than the undescribed *Trypetesa* species and *R. lecointrei,* whose burrow apertures are as adjustable as those of *L. viatrix.* The Carolinian *Trypetesa* is barely attached to the distal end of the burrow, but part of the mantle remains at the initial site of attachment. The peduncular rudiment is free to grow and elongate as the body and the opercular part of the mantle move farther from their initial position.

The last stage in this sequence is the loss of calcareous structures altogether (e.g., *A. utinomii, L. spinatus*). Possibly most extant acrothoracicans fall into this category. However, aside from the presence of chitin (exuvia), the composition of few cement discs is known, and we suspect a facultative ability to produce a short, mineralized cement roof may not be uncommon, given the obvious advantages of post-settlement reorientation.

PALEOBIOLOGY

There are three important considerations that emerge from the foregoing: 1) Acrothoracicans first appeared in the Paleozoic and apparently occupied a greater variety of skeletal substrates in the Mesozoic than they do today [brachiopods, belemnites, and echinoids as well as corals, bryozoans, and gastropod and bivalve mollusks, for example (Tomlinson 1969)]. At least part of this additional diversity was due to species with hard parts (*Rogerella* in echinoid tests); 2) acrothoracicans with obvious calcareous hard parts were apparently more abundant in shallow water in the Mesozoic and Tertiary than they are today; and 3) extant shallow-water acrothoracicans with calcareous hard parts tend to occupy relictual regions such as New Zealand (*Australophialus*), or biogeographical transition zones (*Trypetesa*; Newman 1979), while those with the most primitive or plesiomorphic calcareous hard parts are found in the deep sea (*Weltneria* species and *Lithoglyptes* species). All this suggests that hard parts have not been evolutionarily favored except in certain refugial habitats. Whether this has to do with small size as a refuge from predation in most extant acrothoracicans (those with calcareous

parts tending to be relatively large), or to more subtle metabolic or energy budget-related causes, is unclear.

It was noted above that the calcareous hard parts of *Lithoglyptes viatrix* from the Pacific were very similar to those of a Lower Miocene form from Hungary, described and figured by Zapfe (1936). This is not surprising because, as Fleming (1979) has pointed out, much of the Tertiary marine fauna of the Indo-Pacific, replacing that which became extinct in the Cretaceous, is Tethyan and holds its closest known affinities with the Tertiary marine fauna of Europe.

Conclusions

We have distinguished several different kinds of acrothoracican burrows and calcareous structures associated with them, and discussed the implications for the behavior and morphology of the housed barnacles. These findings apply equally well to extant and fossil burrows, for we have discovered living analogies among several unusual kinds of fossil acrothoracican burrows. Neontologists should now be able to correctly interpret acrothoracican extra-mantle structures, and paleontologists can use such structures to better reconstruct the morphology, life style, and ecological pressures on the barnacles that once inhabited the burrows they may find.

Acknowledgments

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